Spatial and temporal structure in fish distributions: A Lake Ontario case study

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Introduction

Aquatic environments are a heterogeneous patchwork of physical and biological features, much like terrestrial landscapes. In aquatic landscapes, "structure" can be defined as the collective arrangement and configuration of these features (Kracker, 1998). We suggest that heterogeneity in the aquatic landscape, quantified by partitioning spatial and temporal variance in fish distributions, reveals a structure indicative of the underlying ecological processes. Lake Ontario is a three-dimensional, heterogeneous environment exhibiting a structure comprised of temperature gradients, geomorphological elements, and temporally and spatially diverse biota and habitats (Olson et al., 1988; Goyke and Brandt, 1993). Studies of the Laurentian Great Lakes have evolved from whole-lake, homogeneous approaches (e.g., Kitchell et al., 1977; Rand et al., 1995) to partitioning the ecosystem, thereby increasing spatial resolution (Sklar and Costanza, 1991; Brandt

and Kirsch, 1993; Mason et al., 1995). This trend reflects the greater emphasis that has been placed on the importance of scale, pattern, and variation of biological quantities in ecological processes (Petitgas, 1993; Horne and Schneider, 1995; Syrjala, 1996; Kracker, 1997). Environmental heterogeneity plays an important role in ecosystem function by influencing the flow of energy within and among trophic levels (Turner and Gardner, 1991). Spatial and temporal heterogeneity of aquatic resources is driven by processes such as solar energy input, diel migrations by aquatic organisms, aggregative behavior of fish, and water movement. The link between physical features (e.g., thermal structure) and biological processes (e.g., food consumption and resulting growth) has been identified as a crucial aspect of ecosystem dynamics that controls the abundance, distribution, and production of zooplankton and fish populations (Platt and Denman, 1975; Wiebe et al., 1996). Spatially explicit bioenergetics models were developed to couple biological and physical factors under specific environmental conditions (Brandt, 1993; Brandt and Kirsch, 1993; Luo and Brandt, 1993; Horne et al., 1996). Retaining spatial information about the organization of predators and their prey and variation in habitat characteristics contributes to our understanding of bioenergetic processes.

Studies of aquatic environments involving fishery surveys have not routinely included spatial or temporal heterogeneity in analyses of the environment. Traditional sampling methods, such as trawling, are not capable of retaining fine scale spatial or temporal environmental variation in samples but do provide information on abundance and species composition. Biological metrics (e.g., length, age, maturity, stomach contents) and estimates of fish density within a sampled volume can be calculated from catch data, but this offers little information on the spatial and temporal arrangement or heterogeneity of organisms within the sampled volume. Underwater remote sensing is an important tool to retain spatial and temporal information on biological distributions in aquatic environments (Kracker, 1999). Quantifying patterns of biological and physical features using three- or four-dimensional models provides a more realistic representation of aquatic systems.

Underwater acoustic data provide fine-scale (typically less than 5 m vertical, 50-100 m horizontal) resolution (e.g., Greene et al., 1991; Megard et al., 1997) of fish densities over large geographic areas and long time periods to enable the linking of spatial and temporal processes. Underwater acoustic systems sample the water column quickly and efficiently, providing continuous data over large areas (Fig. 1). Acoustic methods have been used in marine ecosystem research since the 1930s (MacLennan and Simmonds, 1992; Brandt, 1996) and in the Laurentian Great Lakes since the 1960s (Mason et al., 2001).

In Lake Ontario, alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and stickleback (Gasterosteidae spp.) are the principle planktivores
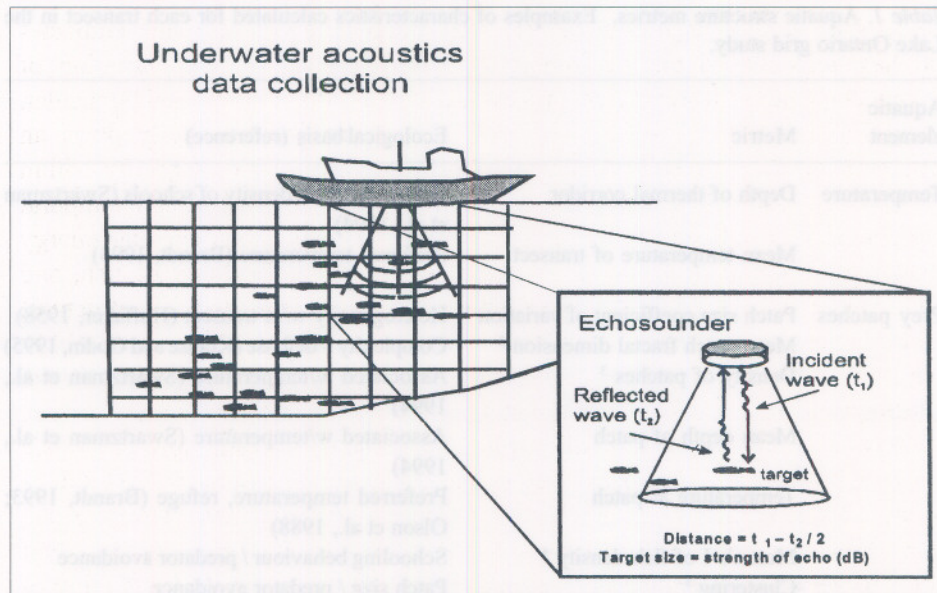
Fig. 1. Schematic depicting acoustic sampling used to produce a two-dimensional view of the spatial distribution of aquatic organisms. The incident wave is reflected off targets in the water column with the strength of the returned signal equivalent to the density of organisms. Used with permission of the Association of American Geographers (Kracker, 1999).

(Brandt, 1986; C.P. Schneider, New York Department of Environmental Conservation, Cape Vincent Fisheries Research Station, N.Y., USA, unpub. data) and they dominate fish biomass in the open waters of Lake Ontario (Urban and Brandt, 1993). These planktivores are the primary prey fish of stocked salmonines, which have had a significant economical value as a commercial sport fishery (Brandt, 1986; Elrod and O'Gorman, 1995; Connelly and Brown, 1991). Lake-wide studies of Lake Ontario's pelagic fish population began in the early 1990s as part of the Lake Ontario Trophic Transfer (LOTT) program and by the Ontario Ministry of Natural Resources (Mason et al., 2001). Following these early LOTT studies, research focus shifted from lake-wide sampling to smaller-scale spatial and temporal studies in the western basin of Lake Ontario (Fig. 2).

We conducted two studies of pelagic fishes in the western basin of Lake Ontario using underwater acoustic sampling to quantify the spatial and temporal variability or structure of pelagic fish distributions. The indices of structure used in this study are the significant scales at which spatial and temporal variance in fish density occurs, as well as ecologically based metrics that address the configuration of biological and physical components of the water column (Table 1). In one study (temporal and spatial spectra study), we installed an acoustic

Table 1. Aquatic structure metrics. Examples of characteristics calculated for each transect in the Lake Ontario grid study.

Aquatic element	Metric	Ecological basis (reference)
Temperature	Depth of thermal corridor	Impact on # and density of schools (Swartzman et al., 1994)
	Mean temperature of transect	Preferred temperature (Brandt, 1993)
Prey patches	Patch size coefficient of variation [1]	Heterogeneity w/in transect (Huffaker, 1958)
	Mean patch fractal dimension [2]	Complexity ~ defense (Krause and Godin, 1995)
	Density of patches [3]	Associated w/temperature (Swartzman et al., 1994)
	Mean depth of patch	Associated w/temperature (Swartzman et al., 1994)
	Temperature at patch	Preferred temperature, refuge (Brandt, 1993; Olson et al., 1988)
	Moran's I of fish density [4]	Schooling behaviour / predator avoidance
	Clustering [5]	Patch size / predator avoidance
	NND [6] to other patches	Heterogeneity w/in transect (Huffaker, 1958)
	NND to predators	Predation pressure
	NND to thermal gradient	Preferred temperature, refuge (Brandt, 1993; Olson et al., 1988)
	Predator-prey coherence [7]	Availability to predator
	Landscape shape index [8]	Complexity ~ defense (Krause and Godin, 1995)
Predators	Temp. in which predator resides	Optimal temp., efficiency of consumption (Brandt, 1993)
	Mean depth of predators	Foraging behaviour / predator demand
	NND to other predators	Competition for prey
	NND to prey patches	Availability of prey
	NND to thermal gradient	Association with optimal temperature

[1] Variation in patch size relative to the mean

[2] The mean perimeter:area ratio of individual prey patches, ranging from simple to convoluted shapes

[3] Number of patches per hectare

[4] Measures spatial autocorrelation (the degree to which nearer features are similar) for fish density within a patch, indicative of compactness of prey patches

[5] The distance at which prey patches are no longer clustered (Getis and Franklin, 1987)

[6] Nearest neighbour distances (NND) are computed for both predator and prey. For instance, the mean distance to the nearest neighbour is calculated between the centre of prey patches and the nearest predator; the centre of prey patches and the thermal gradient; and between one prey patch and another prey patch

[7] Percent area where predator density is greater than the mean predator density and overlaps prey patches

[8] Measure of overall complexity, sum of all boundaries divided by total area (McGarigal and Marks, 1995)
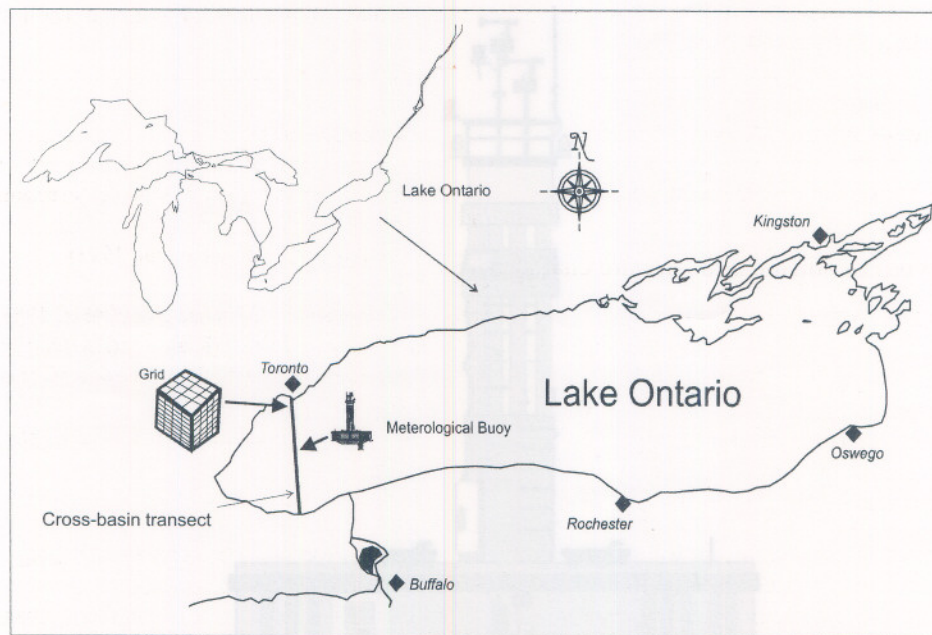
Fig. 2. Locations of the meteorological buoy, cross-basin transect, and grid study sites in the western basin of Lake Ontario.

system on a meteorological buoy and continuously sampled at that point. This same location was sampled during a cross-basin transect for comparative purposes. In the second study (grid study), we sampled fish distribution using underwater acoustics while collecting data on water temperature across a one-nautical mile grid sampled repeatedly over a 24-hour period. Ecological metrics indicative of foraging behavior, defense mechanisms, preferred temperature, etc. were applied to the acoustic transects to address the spatial characteristics and potential interactions between predator, prey, and water temperature. For both studies, the acoustic data were collected at a high spatial and temporal resolution, resulting in a data set of fish distributions in western Lake Ontario over a range of spatial and temporal scales.

Methods

Acoustic data

For both the cross-basin transect and the buoy, a 120 kHz Simrad EY500 Split Beam Echosounder (half power beamwidth = 7.2°, pulse duration = 0.3 msec)
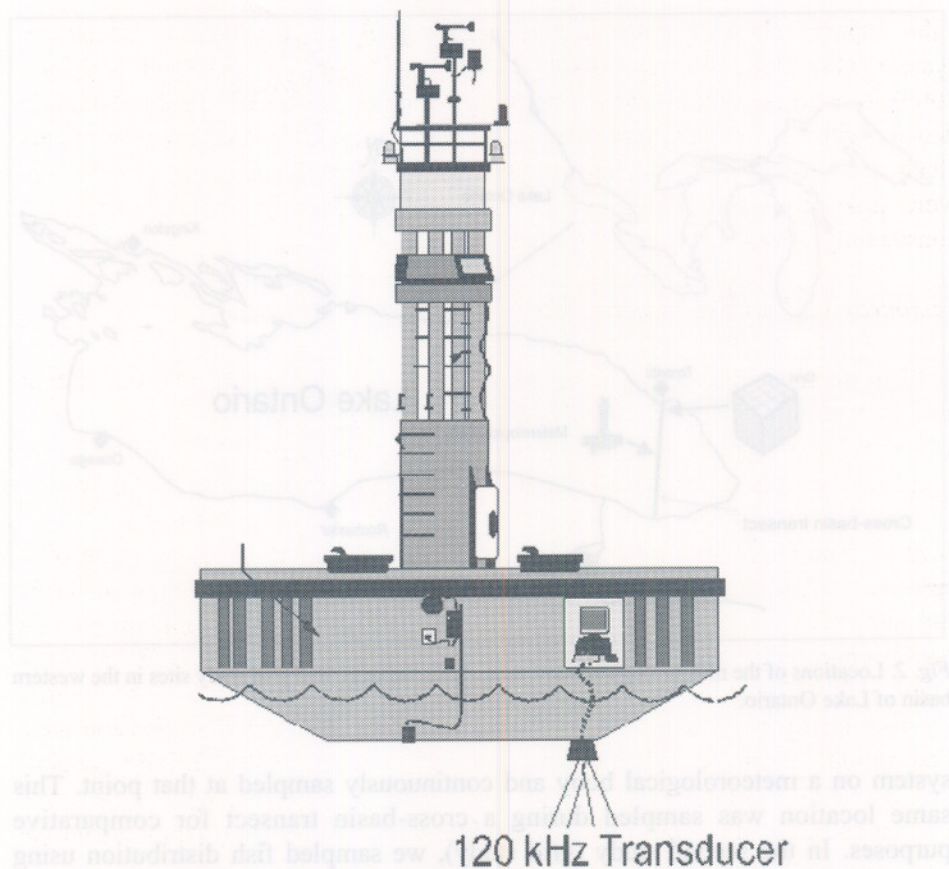
120 kHz Transducer

Fig. 3. Great Lakes Environmental and Acoustic Monitoring System (GLEAMS) anchored in the western basin of Lake Ontario (43° 14.7N, 79° 13.1W) used to continuously sample meteorological, physical, and biological variables. During June, 1996 the buoy was outfitted with a Simrad 120 kHz split beam echosounder. The buoy was operated and maintained by the Canadian Centre for Inland Water (Burlington, Ontario).

was used to collect acoustic data. The acoustic data for the grid study was collected using a 120kHz dual-beam Biosonics 102 Echosounder (half power beam width = 10° and 25°, pulse duration = 0.3 msec). The transducer actively transmits a pulse of sound and listens for echoes reflected from targets in the water column (Fig. 1). Acoustic backscatter is proportional to the density of organisms. The echosounder was calibrated before each sampling session using a tungsten-carbide reference sphere (Foote, 1982; MacLennan and Simmonds, 1992). The reference target was placed beneath the transducer and moved within each quadrant of the beam so that the beam pattern could be accurately described. Measured target strength (TS) values were compared to a reference

value (sphere diameter = 19 mm, TS = -40.4 dB at 120 kHz) to adjust the system calibrations. Acoustic data were processed using DEVIS (Jech and Luo, 2000) to estimate spatial and temporal arrays of numeric fish density. Numeric density within array cells was calculated using in situ individual target strengths (Jech and Horne, 2001). Acoustic data collected on the meteorological buoy were post-processed to remove echoes from the buoy's mooring chain (a consistently strong echo at a constant depth).

Temporal and spatial spectra study

A 12 m diameter meteorological buoy (Fig. 3) was used for the high-resolution temporal sampling. The meteorological buoy was located in the western basin of Lake Ontario south of Toronto in 110 m of water at 43°14.7N, 79°13.1W (Fig. 2). The split-beam transducer was mounted in a well through the bottom of the buoy at a depth of 1.5 m. Data were collected continuously for seven days in June (June 10 14:57 EDT to June 17 23:52 EDT, 1996) at a rate of 1 pulse sec^{-1}. Acoustic data were horizontally averaged into one-minute intervals and integrated in 0.5 m vertical bins. Fish lengths were computed using Foote's (1987) empirical relation between target strength (TS, units dB) and fish total length (TS (dB) = 20log(Lcm) - 71.9). Temporally-indexed data were also divided into four time periods to examine the effect of sunlight on fish densities and their distribution. "Dusk" was defined as the period between 2130 -2229 hr; "Night" was between 2230 - 0429 hr; "Dawn" was 0430 – 0529; and "Day" was defined as 0530 -2129 hr. These categories were chosen using nautical sunrise and sunset times during June.

A 50 km cross-basin transect was acoustically sampled during the night of August 25, 1996. Pelagic species tend to disperse and vertically migrate from bottom to surface during dark hours, which improves the resolution of individual animals (Brandt et al., 1991). The transect intersected the position of the meteorological buoy (Fig. 2). During the transect, the transducer was mounted on a dead-weight tow body suspended 1.5 m under the surface of the water alongside the research vessel, with a sample rate of two pulses sec^{-1}. Acoustic data were averaged across 40 m horizontally and integrated in 0.5 m vertical bins. The vertical thermal structure of Lake Ontario was measured at ten locations along the transect and at the buoy during acoustic data collection. Temperature profiles were vertically averaged in 0.5 m bins and linearly interpolated across 40 m horizontal intervals.

To examine the effect of thermal structure on fish density distributions, we separated the acoustic data into three vertical strata. The epilimnion stratum ranged from 1.5 m below the surface to the top of the thermocline. The metalimnion stratum encompassed the thermocline. The hypolimnion stratum

was the uniform temperature water between the thermocline and the lake bottom. The water column was also processed as a single integrated stratum to compare stratified results with the entire water column.

We used spectral analysis (Jenkins and Watts, 1968; Platt and Denman, 1975; Chatfield, 1980) to statistically analyze variance in fish densities and examine scales of spatial and temporal variability. We partitioned the variance of fish density among the observed spatial (wave numbers) or temporal (frequencies) scales. Peaks in the spectrum are biologically interpreted as the dominant scales within the spatial or temporal series (Horne and Schneider, 1995). A white noise analysis and a fast Fourier transform (FFT) were used to examine temporal and spatial patterns at individual depth strata and over the entire water column. The white noise analysis used Fisher's KAPPA statistic (Davis, 1941; Fuller, 1976) and Bartlett's Kolmogorov-Smirnov (BKS) test statistic (Bartlett, 1966; Fuller, 1976) to determine if the spectra were significantly different from a random series (i.e. white noise). The FFT analysis identified significant contributions of variance at particular scales. We processed the data through an FFT routine and then smoothed the spectral densities using a weighted triangle filter. The smoothing process specifies the relative weights used in the moving average to form spectral density estimates (Denman, 1975; SAS Institute, 1990). To enable comparison among power spectral curves, all data series were normalized prior to analysis. All statistical analyses were completed using the Statistical Analysis System (SAS) software (SAS Institute, 1990) and Interactive Data Language (IDL) software (Research System Inc., 1995).

Grid study

We designed an acoustic grid survey to investigate the three-dimensional spatial variability in fish distributions and water temperatures over short time periods at an offshore location about three kilometers from Toronto Island (Fig. 2). The grid was composed of five north-south and five east-west transects spaced about 465 meters apart, covering one square nautical mile (1852 m^2). Sampling occurred over a 24 hour period in three seasons (July 1995, October 1995, and April 1996). A single transect represents a 20 minute snapshot of fish distribution through the water column. A complete grid of ten transects was sampled every four to six hours and was repeated throughout a 24-hour period resulting in four complete grids in each of the three seasons. Acoustic data were integrated horizontally over 30 m and vertically over 1 m bins.

The physical characteristics of the Lake Ontario grid site included a bottom depth of 40 to 60 meters and a "thermal corridor" with an average depth of 6.2 meters. For the purposes of the grid study, we defined the "thermal corridor" as water temperature between 12° to18°C. This definition is ecologically significant

because it is the preferred temperature range in which salmonids can realize at least 50% of maximum consumption (Stewart and Ibarra, 1991) and assuming that food is available, will result in fish growth.

The intensity or target strength (TS, units dB) of the backscattered echo from individual targets was used to estimate the length of individual fish by applying Love's TS-length regression (Love, 1977). Fish targets were separated into appropriate classes representing predators and prey. In this case, predators were defined as targets greater than 225 mm in length (Goyke and Brandt, 1993) and prey patches were defined as contiguous cells with prey fish density greater than 0.7 times the average density within a transect. Water temperature data were collected using a Seabird-19 conductivity-temperature-depth (CTD) recorder towed to allow the CTD to ascend and descend between the surface and the bottom along the cruise track (Stockwell and Sprules, 1995). Water temperature was horizontally interpolated at 30 m intervals to match the resolution of the acoustic data. When all data were combined, we had spatially-explicit maps of (a) fish densities, (b) water temperature, (c) and predator location (Fig. 4). Metrics that facilitate interpretation of ecologically significant patterns were used to quantify the spatial arrangement of biological and physical characteristics of each transect (Meaden, 1996; Petitgas, 1996; Kracker, 1998). For example, nearest neighbor distances (NND), clustering (distances at which prey fish are no longer clustered), and Moran's I (a measure of spatial autocorrelation where features that are closer to each other tend to be similar) were selected to characterize schooling, avoidance behavior, and potential predator-prey interactions (cf. Table 1). All metrics were calculated using IDL (Research System, Inc., 1995), ArcInfo/ArcView (ESRI, 1997), Fragstats (McGarigal and Marks, 1995) and S-Plus (MathSoft Inc., 1997). The metrics were used to characterize the configuration of biological and physical features within each transect and to differentiate classes with similar characteristics using principal component analysis (PCA) in S-Plus (MathSoft Inc., 1997). PCA is a data reduction technique that summarizes correlated variables into a few categories that best describe variability in the entire dataset (Dunteman, 1989). Variables that load highly on each principal component have a strong association with that category and indicate the dominant characteristics for that category or type of aquatic structure.

Results

Temporal and spatial spectra study

Temporal fish density was defined as fish abundance per unit volume per minute (or per hour) measured at the site of the GLEAMS buoy. During the seven day
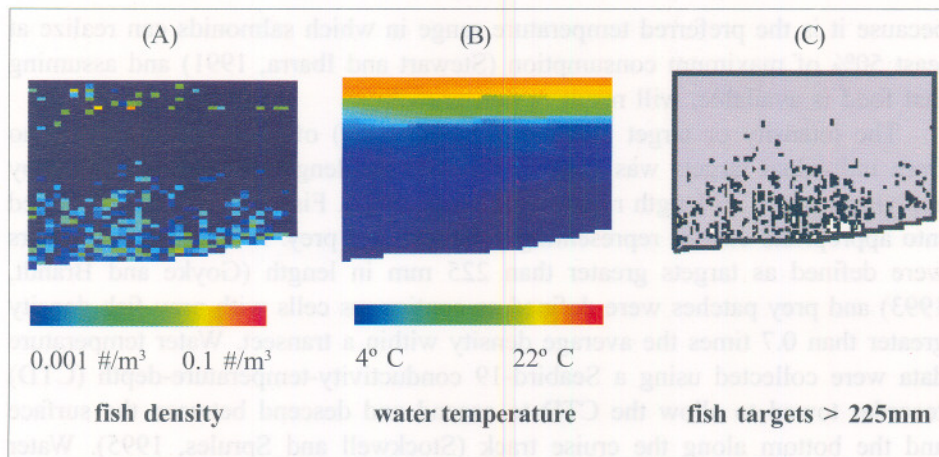
Fig. 4. Spatial distribution maps of fish density, water temperature, and large fish derived from grid surveys. Transect length = 1852 m (1 nautical mile). Depth range = 40-60 m. Used with permission of the Association of American Geographers (Kracker, 1999).
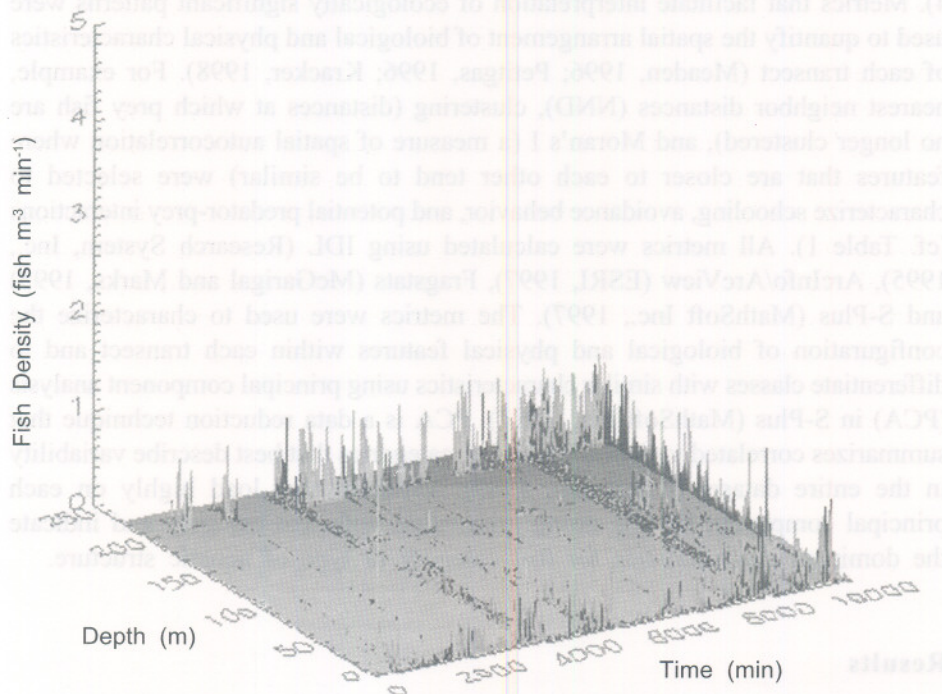

Fig. 5. Three-dimensional (depth, time, fish density) view of acoustic data collection during June 1996 from a meteorological buoy in the western basin of Lake Ontario. Data collection commenced at 1457 June 10th and ended at 2352 on June 17th. Resolution of the view is 1 minute (time) by 1 meter (depth).

data collection, fish densities ranged from 0 to 1.2 fish m^{-3} min^{-1} (Fig. 5). The average fish density for the entire time series was 0.075 fish m^{-3} hr^{-1} (Table 2). Surface temperatures remained near 15 °C, the thermocline depth was less than 10 m deep, and the hypolimnion temperature was consistently near 5 °C. Fish densities varied on a diel cycle where peaks in temporal variance of fish density occurred at temporal scales of 24, 12, and 4 hours (Fig. 6). The metalimnetic stratum had the lowest spectral density among all strata. Spectral densities for the water column and epilimnion strata were similar at all temporal scales. Spectral densities for the hypolimnion stratum were highest across scales greater than 0.5 hours, and were similar to the water column and epilimnion strata at scales less than 0.5 hours. At temporal scales less than one hour, spectral densities were relatively flat for water column, metalimnion, and epilimnion strata.

During the day, fish aggregated near the bottom. The fish began to migrate vertically upwards during dusk and early evening, dispersed during dark hours, and completed the cycle by migrating towards the bottom during late night and dawn. The highest average density occurred during dusk. Daytime had the lowest average densities, but also had the maximum fish density observed. During night, average fish densities and the maximum density were ranked second highest (Table 2).

Along the cross-basin transect, surface temperatures ranged from 14.3 to 23.0 °C (Fig. 7 upper panel). In the southern inshore region, the surface water was generally warmer (21.5 - 23.0 °C). Thermocline depth was shallowest (~2.5 m) along the north shore and gradually deepened to about 20 m at the southern end of the transect. Below about 30 m, temperature was uniformly 4 °C. Fish distribution patterns differed between inshore and offshore regions along the cross-basin transect (Fig. 7 lower panel). Highest densities of fish occurred in the epilimnion and the thermocline throughout the transect. Fish aggregations were observed along the 50 m bathymetric contour at the northern and southern boundaries of the transect. In the southern inshore region, fish

Table 2. Average and range of fish density for night, dawn, day and dusk time periods during the seven day time series

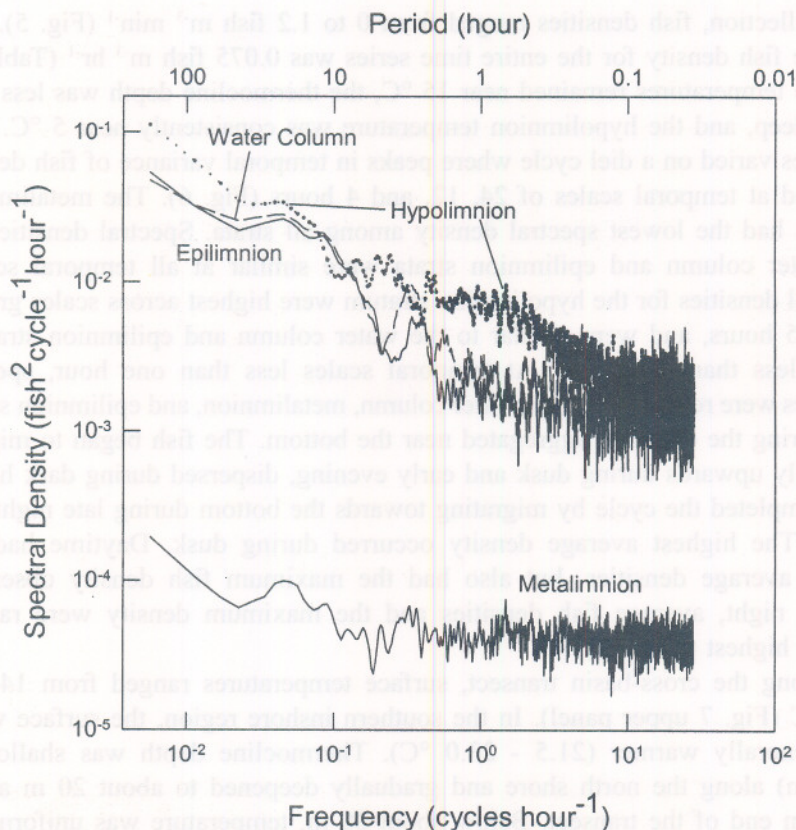| Time period	Average fish density (fish m^{-2} hr^{-1})	Range of fish density (fish m^{-2} hr^{-1})
Night	0.092	0.031 - 8.22
Dawn	0.088	0.031 - 3.41
Day	0.014	0.029 - 9.42
Dusk	0.107	0.032 - 5.91
Entire day	0.075	0.029 - 9.42

Fig. 6. Spectral density estimates for the time series of fish densities collected during June 1996. Spectral density is plotted as a function of frequency (centred and normalised, lower axis) and period (upper axis). Spectral estimates of the three thermal strata (epilimnion-solid line, metalimnion-solid line, and hypolimnion-dotted line) and entire water column (dashed line) are displayed.

tended to be distributed throughout the water column. In the offshore region, few fish were detected in the hypolimnion.

For the cross-basin transect, spectral density values were lowest in the metalimnion across all scales (Fig. 8). At scales less than 1 km, epilimnetic and hypolimnetic spectral density curves were similar, and values from all strata were relatively flat. At scales less than 10,000 m, spectral density values for the water column were lower than for the epilimnion and hypolimnion strata. Peaks in the spectral density curve occurred from small to intermediate scales along the cross-basin transect for all strata, although specific periods or frequencies were not consistent among strata. Spectral density values from the metalimnion stratum peaked at 0.9, 0.5, and 0.3 km scales, epilimnetic spectral densities
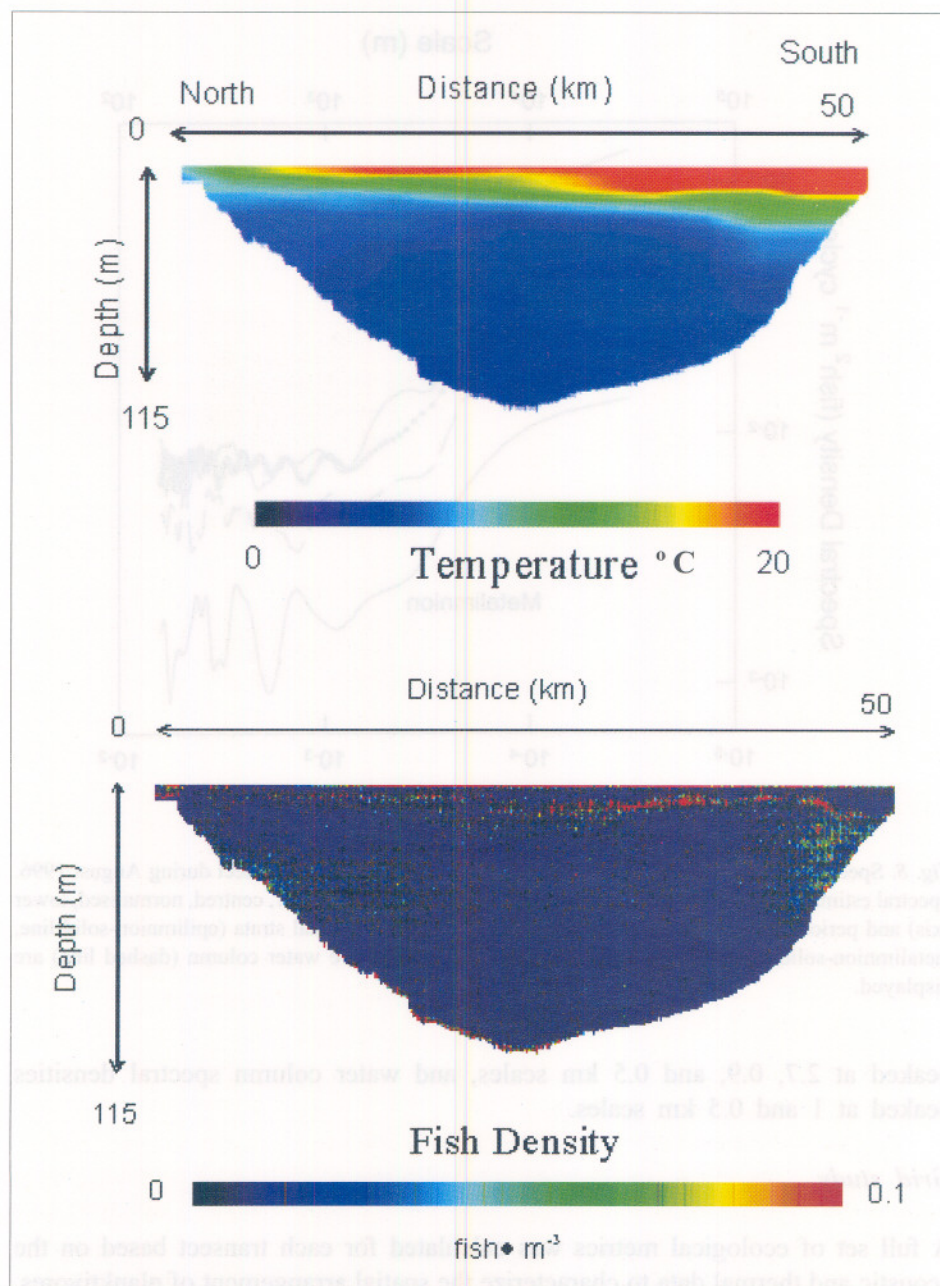
Fig. 7. Two dimensional view of water temperature (upper panel) and fish densities along the cross-basin transect during August 1996. Temperature was linearly interpolated among vertical temperature profiles. Data collection commenced at the north end of the transect at 2213 (EDT) on August 25 and ended at 0337 on August 26. Spatial resolution of the view is 40 m horizontal x 0.5 m vertical.
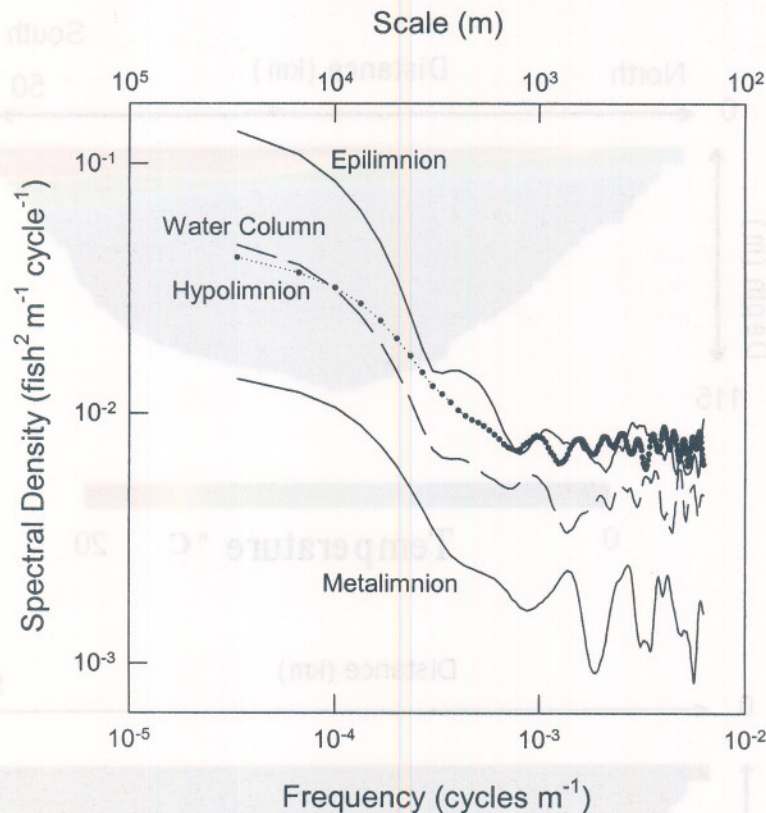
Fig. 8. Spectral density estimates of fish densities for the cross-basin transect during August 1996. Spectral estimates are plotted as a function of frequency (bandwidth 0.01, centred, normalised, lower axis) and period (upper axis). Spectral estimates of the three thermal strata (epilimnion-solid line, metalimnion-solid line, and hypolimnion-dotted line) and entire water column (dashed line) are displayed.

peaked at 2.7, 0.9, and 0.5 km scales, and water column spectral densities peaked at 1 and 0.5 km scales.

Grid study

A full set of ecological metrics was calculated for each transect based on the acoustic and thermal data to characterize the spatial arrangement of planktivores, water temperature, and piscivores in the Lake Ontario grid (Table 1). Principal components analysis (PCA), using the suite of spatial/ecological metrics as variables, was used to determine which structural characteristics differentiate one category or type of transect from another. Principal components analysis of

all metrics for three seasons revealed strong seasonal variability in water temperature and fish abundance, masking the dominant spatial structure evident in any one season. Further PCA analysis with a set of 19 metrics that specifically addressed the spatial configuration of features in the July grid defined four significant categories of aquatic structure for this season. These first four components accounted for 68 percent of the variability in the July data and identify characteristics that are most important in differentiating categories or types of transects (Table 3). The four types of aquatic structure are characterized by: 1) complex structure, 2) deep prey patches with predators, 3) dominance of thermal corridor, and 4) sparse water column.

Discussion

These studies explore the premise that aquatic structure reflects underlying, ecologically significant processes (Turner and Gardner, 1991). Results of the spectral analyses and grid studies delineate distinct spatial and temporal patterns in the aquatic structure of Lake Ontario. Distinct peaks of temporal variance in fish density were observed at the scale of diel, semi-diel and 4 hour time periods, with the thermocline stratum explaining the greatest variation in fish density. This pattern suggests behavior associated with vertical fish migration and a response to the thermal gradient.

The categories of aquatic structure differentiated as a result of the grid analysis also indicate quantifiable structure in the aquatic environment. The first type of aquatic structure is characterized by complexity and is evident in nighttime transects. In this category, fish are distributed throughout the water column, patch size is variable, and the patchiness of prey results in a biological environment that is geometrically complex, as measured by fractal dimension. This structure is most complex before and after midnight and less complex around midnight. The structure of these transects is also characterized by very high coherence between predators and prey, where a high percentage of the transect has prey patches that coexist with predator densities greater than the mean. Transects that fall into this type of structure are observed in the middle of the night (Fig. 9). Large, deep prey patches and short distances between predator and prey characterize the second type of aquatic structure. This category is observed during dawn and dusk periods. Distances between fish and the thermal corridor were large during these times. At dawn and dusk, predator and prey were typically found in the lower portion of the water column. While predators and prey coincided deep in the water column, prey were aggregated in large patches, and predators were a large distance from their optimal bioenergetic growth temperature. This spatial distribution may influence the efficiency of prey capture,

Table 3. Results of principal components analysis identified four distinct types of aquatic structure based on a suite of ecological metrics defining the spatial characteristics of individual transects.

	Types of aquatic structure in thermally stratified transects (Cumulative variation explained)			
	I. Complex structure (0.32)	**II. Deep prey patches with predators** (0.498)	**III. Dominance of thermal corridor** (0.587)	**IV. Sparse water column** (0.666)
Spatial characteristics determining type of aquatic structure (loading or weight of association)	Mean temperature in which predator resides (0.301)	Mean depth of patch (0.390)	Mean temperature of transect (-0.523)	NND coefficient of variation for patches (0.484)
	Mean patch fractal dimension (-0.295)	Mean nearest neighbor distance (NND) patch to thermal corridor (0.368)	Depth of thermal corridor (-0.522)	Landscape shape index (-0.360)
	Predator-prey coherence (-0.278)	Mean depth of predator (0.344)	Standard deviation of NND of predator to thermal corridor (0.265)	Largest patch index (-0.334)
	Distance to nearest predator from each cell in the transect (0.264)	Mean NND of predators to thermal corridor (0.308)	Moran's I of fish density within patches (-0.224)	Kurtosis of fish density frequency distribution (-0.332)
	Patch size coefficient of variation (-0.252)	Clustering (distance at which patches are no longer clustered) (0.306)	Standard deviation of NND of patch to thermal corridor (0.208)	Standardized NND of patches (-0.299)

consumption, and resulting predator growth. The degree of clustering or aggregation of fish may also have implications for predator feeding success. More compact schools of prey may decrease the ability of predators to recognize and capture food (Krause and Godin, 1995). These characteristics were most evident as planktivores ascended and descended in the water column.

The third type of aquatic structure describes daytime characteristics. Fish were sparsely distributed through the water column and the thermal corridor
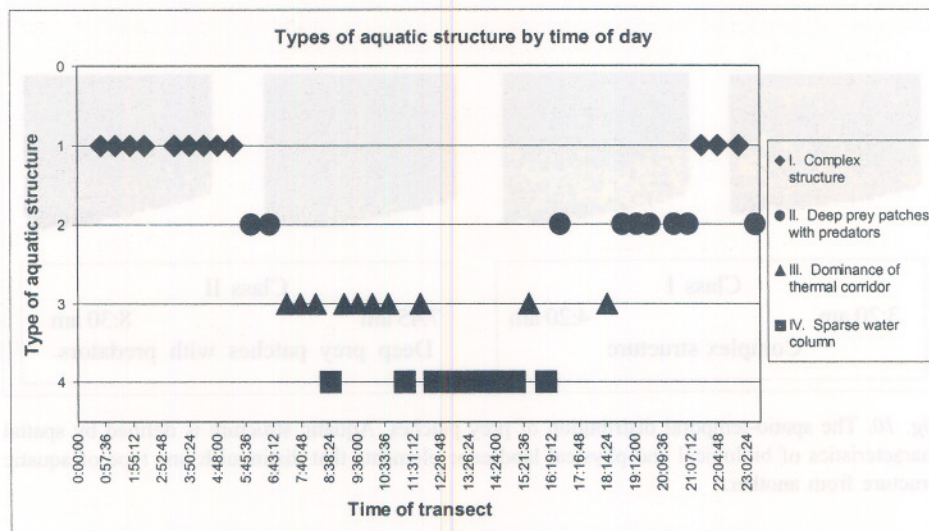
Types of aquatic structure by time of day

Legend:
- ♦ I. Complex structure
- ● II. Deep prey patches with predators
- ▲ III. Dominance of thermal corridor
- ■ IV. Sparse water column

Y-axis: Type of aquatic structure (0, 1, 2, 3, 4)
X-axis: Time of transect

Fig. 9. PCA scores from July transects cluster into distinctive types of aquatic structure related to time of day.

extended to a maximum depth of nine meters during mid-morning. With most fish near the bottom during the day, little variability existed in predator and patch distances to the thermal corridor. The fourth class of aquatic structure further defines daytime transects and reflects a sparse water column with few fish. This differentiation of distinct types of aquatic structure parallels temporal changes (Fig. 10) that occur with diel vertical migration. Specifically, the complex structure of the first category of transects coincided with the heterogeneous distribution of prey throughout the water column at night. Dawn and dusk (class II) coincided with compact prey patches ascending and descending through the water column. Classes III and IV reflected sparse daytime transects where the dominant feature in the aquatic landscape was the thermal corridor. The structure identified through this approach provides a view of the distributions and interrelationships of both biological and physical elements that comprise aquatic landscapes.

The two case studies presented in this paper focused on the investigation of spatial and temporal characteristics to identify and delineate aquatic structure (i.e., a specific arrangement of resources). Our results show that the spatial arrangement and density of pelagic fishes and water temperature exhibits unique spatial characteristics occurring at distinct times within a 24 hour period. We identified distinct types of aquatic structure and detected changes in the spatial and temporal arrangement of water temperature, planktivores, and piscivores. The transition of spatial characteristics and the configuration of aquatic landscape
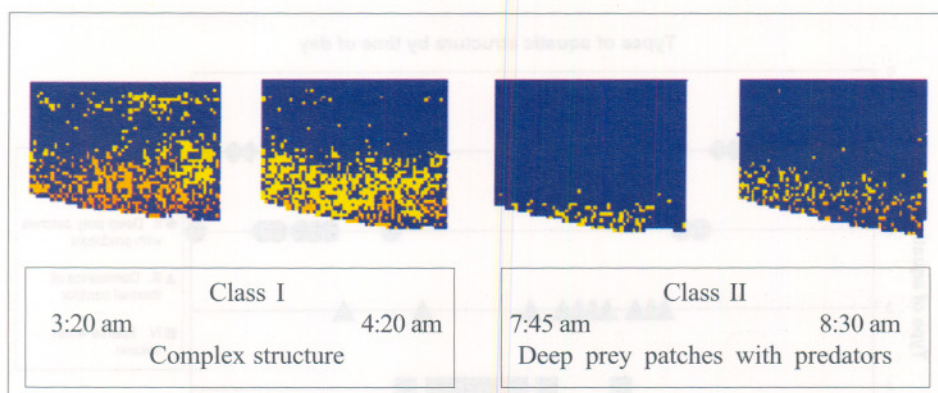
Class I	Class II
3:20 am 4:20 am	7:45 am 8:30 am
Complex structure	Deep prey patches with predators

Fig. 10. The spatio-temporal distribution of prey patches. Aquatic structure is defined by spatial characteristics of biological and physical landscape elements that distinguish one type of aquatic structure from another.

elements over a 24-hour period paralleled underlying ecological processes such as diel vertical migration and schooling. This approach is useful for defining the changes in fish distribution in relation to the physical features of the water column (depth, distance from thermocline, proximity to the bottom and availability of prey). Changes in structure likely impacts ecological function. To illustrate by example, during vertical migration, complexity of aquatic structure and variability in patch size may offer more opportunities for capture by predators or more success in avoiding predators by prey (Krause and Godin, 1995). The effect of changes in aquatic structure on a predator's ability to capture and efficiently use prey can now be defined and quantified using metrics that capture variability that likely affects consumption and growth. Bioenergetic models that examine spatial coincidence of predator, prey, and "preferred" temperature must also include changes in aquatic structure at temporal resolutions that are biologically meaningful to foraging.

In addition, this work defines the temporal and spatial scales at which conditions are no longer homogeneous. That is, we provide a basis for determining the spatial and temporal resolution that should be used as a minimum sampling unit to capture accurate measures of fish densities and characterize fish behavior within the context of diel vertical migrations. Using acoustic survey data, we were able to capture fine-scale transitions in aquatic structure from deep prey patches coinciding with predators, to complex aggregations of prey, and then to more dispersed distributions of prey. Likewise, the observed cycle of distinct periods of variance in fish density at the moored location is consistent with models of diel vertical migration (Mangel and Clark, 1988) and provides direct evidence of the time scale at which this occurs. This study provides a model for examining the spatial and temporal distribution of fish and water temperature in

the three-dimensional water column and the impact of that organization on ecological processes.

Conclusion

Quantifying the spatial and temporal heterogeneity of biological resources and physical features is a step towards understanding ecological functions within the aquatic environment. Underwater acoustics, along with measures that recognize spatial and temporal heterogeneity, provide the requisite tools for defining the aquatic environment at an appropriate scale and understanding the effect of structure on predator-prey interactions. Results from these studies illustrate approaches to incorporate high-resolution information on biological distributions and aquatic structure into investigations of Lake Ontario fisheries. In addition, this work provides a framework for improved population assessments by partitioning variance as a quantitative measure of heterogeneity in fish distribution. While these analyses do not include all ecological interactions within the transects or during a seven day time series, they present consistent spatial and temporal relationships that can be further evaluated for their impact on ecological function and to better understand how pelagic fishes utilize the aquatic habitat.

Summary

Spatial and temporal variation or heterogeneity within ecological systems plays an important role in maintaining populations and influencing the flow of energy and materials (Huffaker, 1958; Turner and Gardner, 1991). The spatial and temporal configuration of physical and biological features comprises the "structure" of the aquatic environment. In this study, we define aquatic structure by quantifying the patterns and relevant scales of spatial and temporal variance in these ecosystem components, which leads to hypotheses on the underlying processes and the influence of heterogeneity on ecological function. Fisheries research using acoustics facilitates real-time sampling of the distribution and potential interactions of aquatic organisms and retains fine-scale information about their organisation in space and time. This paper describes two studies conducted in the western basin of Lake Ontario designed to investigate spatial and temporal distributions of pelagic fishes and the factors influencing their distribution. One study uses spectral analysis to examine scale-dependent temporal patterns in fish distributions. The second study describes spatial patterns in temperature and fish distribution using high resolution sampling of a three-dimensional grid. These studies found that biological and physical elements within the aquatic environment exhibit a quantifiable spatial arrangement or "structure"

that varies with time of day. These results provide a model to examine variation in spatial and temporal distributions of biological and physical components of aquatic environments in three and four dimensions and the resulting impact of structural organisation on bioenergetic processes.

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